



# Reduced orbitofrontal cortical volume is associated with interdependent self-construal

Shinobu Kitayama<sup>a,1</sup>, Kuniaki Yanagisawa<sup>b</sup>, Ayahito Ito<sup>c</sup>, Ryuhei Ueda<sup>d</sup>, Yukiko Uchida<sup>b</sup>, and Nobuhito Abe<sup>b</sup>

<sup>a</sup>Department of Psychology, University of Michigan, Ann Arbor, MI 48103; <sup>b</sup>Kokoro Research Center, Kyoto University, Yoshida Sakyo-ku, Kyoto 606-8501, Japan; <sup>c</sup>Kansei Fukushi Research Institute, Tohoku Fukushi University, Aoba-ku, Sendai 989-3201, Japan; and <sup>d</sup>Graduate School of Letters, Kyoto University, Sakyo-ku, Kyoto 606-8501, Japan

Edited by Susan T. Fiske, Princeton University, Princeton, NJ, and approved June 21, 2017 (received for review March 23, 2017)

Interdependent self-construal refers to a view of the self as embedded in relationships with others. Prior work suggests that this construal is linked to a strong value placed on social obligations and duties. Interdependent people are therefore cognitively attuned to others and various social events in their surroundings while down-regulating their personal goals. In the present work, we examined whether structural properties of the brain predict interdependent self-construal. We performed a structural magnetic resonance imaging on 135 Japanese young adults while assessing (i) independent and interdependent self-construals and (ii) the degree to which individuals form vivid images of external objects (object imagery). The cortical volume of the orbitofrontal cortex (OFC) (a core cortical region responsible for value-based decisionmaking and, thus, inherently involved in personal goals and desires) inversely predicted interdependent self-construal. Further analysis found that the highest level of interdependent self-construal is achieved when those who are relatively low in the OFC volume are simultaneously high in object imagery, consistent with previous evidence that interdependence, as realized via obligation and duty, requires both the reduced self-interest and vigilant cognitive attunement to environmental context.

interdependence | orbitofrontal cortex | self-construal | voxel-based morphometry

Humans are social animals. They constantly interact with conspecifics and survive by forming large social groups (1, 2). Although how they may do so is a matter of debate, it is instructive that two distinct construals of the self and social relations, called independent and interdependent, are common across cultures and considered instrumental in both forming social relations and anchoring agency in these relations (3, 4). The independent construal of the self involves a focus on self-interest. As Adam Smith (1776) argued more than two centuries ago, this pursuit of self-interest can result in mutually satisfying social relations (5). In contrast, interdependent construal of the self involves a commitment to duties and obligations, in addition to attendant feelings of sympathy and comradeship (3). Thus, interdependent people are closely attuned to various other-related cues in the environment and prepared to act on behalf of the others so as to meet their expectations and to abide by norms of reciprocity with them. Further, they may also temper and temporarily suspend their self-interest.

The formation of social relations through interdependence has long been acknowledged. For example, as early as in 1871, Darwin posited that prosocial tendencies were essential building blocks of sociality (6). It might come as surprising that in modern elaborations of Darwin's principles in psychology, biology, and economics, scholars often assume that the altruistic orientations are unlikely to persist in a population because those who take altruistic orientations would be exploited and outproduced by nonaltruists (7). These claims notwithstanding, there has now emerged an increasing recognition that the prosocial, interdependent orientation may prosper (8) as long as strong social norms are established in a local community such that the pursuit of self-interest is strongly punished (9). Moreover, social norms

that value reciprocity or communal sharing of favors may often be internalized. We may therefore expect that the interdependent construal of the self may thrive in a community in which each member's self-interest is chronically suspended or reduced. Moreover, once the interdependent, prosocial behavioral tendencies toward duties and obligations are established, they are likely to further decrease the propensity toward personal goal pursuit.

Here, we build on this line of thinking and examine whether the volume of certain cortical regions linked to personal goal pursuit would be inversely associated with an interdependent construal of the self. We hypothesize that interdependent social relations occur when individuals in the relations are closely attuned to others' needs or desires, and social norms for reciprocity and sharing while automatically tempering their personal goals and priorities. One of our key target areas was the one involved in the processing of goals and desires of the self (e.g., the orbitofrontal cortex, OFC) (10–12).

## Regulating Self-Interest

Interdependent relations that are anchored in the sense of duty and obligation can be sustained when there is a strong assurance that individuals in the relations do not act selfishly and, thus, do not exploit those who act in a more prosocial fashion. Norms against selfish behaviors are often instrumental in sustaining this expectation and assurance (13). A recent study shows that under such conditions, there could emerge spontaneous psychological

## Significance

Recent work in cultural neuroscience suggests that socio-cultural processes are reciprocally influenced by neural mechanisms that are recruited to support social behaviors. In particular, interdependent orientations (which include a commitment to duties and obligations, and prosocial tendencies) require both the suspension of self-interest and cognitive attunement to social surroundings. Dominant theoretical perspectives suggest that this orientation is achieved through active inhibitory control of egoism. Our results highlight an alternative pathway wherein the suspension of self-interest is achieved through reduced cortical volumes for personal incentives and goals. This reduced cortical volume is linked to interdependence especially for those who are cognitively attuned to the surrounding context. Therefore interdependent tendencies may be automatic and supported by structurally realized inhibition of egoism.

Author contributions: S.K., Y.U., and N.A. designed research; K.Y., A.I., R.U., and N.A. performed research; K.Y., A.I., R.U., and N.A. analyzed data; and S.K. and N.A. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: The data reported in this paper have been deposited in Neurovault ([neurovault.org/collections/2486](http://neurovault.org/collections/2486)).

<sup>1</sup>To whom correspondence should be addressed. Email: [kitayama@umich.edu](mailto:kitayama@umich.edu).

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1704831114/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1704831114/-DCSupplemental).

propensities to act in accordance with the other-centric or prosocial norms favoring obligations and duties to others over pursuit of personal goals. Young American adults with either European or Asian ancestry performed a simple cognitive task as fast and as accurately as they could to earn points for either themselves or their best friends (14). The researchers examined the magnitude of error-related negativity (ERN), an event-related potential component that is contingent on errors made on the cognitive task, interpreted as an index of motivational engagement. The key index was the relative size of the ERN in the self condition versus the ERN in the friend condition, termed the self-centric effect. As may be expected, the amplitude of the ERN in the self (versus friend) condition was negatively associated with interdependent self-construal. Moreover, this association between the prosocial tendency, as indexed by a smaller self-centric effect, and interdependent self-construal explained an overall cultural difference. Compared with those European backgrounds, those with Asian backgrounds were relatively more interdependent, which in turn explained their prosocial propensity toward their best friends (vs. the self).

To the extent that relatively weak motivational engagement to the pursuit for personal desires and goals is an important element of interdependent self-construal, one may expect cortical regions implicated in the desires and goals of the personal self to be closely linked to this individual difference variable. One region that is particularly important is the OFC. Previous animal work shows that OFC lesions result in difficulties associating reward values to various contextual cues (10). Among humans, individuals with OFC lesions have difficulty in reversing instrumental conditioning or sustaining an internally consistent set of personal preferences (10). Further, OFC is closely implicated in the calculation of rewards and punishments associated with any given action of the self (15) and, thus, is likely critical in navigating the self in the social world (16). We thus hypothesize that one prominent function of the OFC is to promote the identification and maintenance of goals and desires or, more generally, self-interest (11, 12). Conversely, lowering of this OFC function, as characterized by the decreased regional gray matter volume, may be linked to interdependence that is realized through obligation, duty, and attendant inhibition of self-interest. Further, people committed to this form of interdependence may be expected to constantly down-regulate their self-interest.

The last decade of research on neuroplasticity shows that the gray matter volume of relevant cortical regions can change systematically as a function of spatial navigation (17), and long-term practice in a spatio-motor coordination task such as juggling (18), games such as chess and GO (19), and musical instruments (20). Further support for the hypothesis that social relations can modulate structural properties of the brain comes from a systematic relationship between social network size and the volume of the amygdala and certain paralimbic regions (21). To the extent that interdependence entails less active recruitment of OFC functions, there may result a reduction of the OFC volume.

Wang et al. recently examined Chinese young adults and tested whether independent and interdependent self-construals would predict the cortical volume in different brain regions (22). The researchers used a difference score between interdependent and independent self-construal and, yet, they evidently found that much of the effect of this difference score was due to interdependent self-construal. One key finding was that interdependent self-construal inversely predicts the volume in the ventral medial prefrontal cortex (vmPFC). Because part of vmPFC overlaps with OFC, this finding can be seen as supportive of our prediction on the OFC volume. Nevertheless, there is one important caveat. The finding does not appear to have survived a stringent statistical threshold [i.e., family-wise error (FWE)

correction at the voxel level] that takes into account the inflation of type I errors in the voxel-based brain imaging data. If nothing else, careful replication is called for.

### Vivid Representations of Others in Social Context

Although we have so far predicted a broad association between reduced OFC volume and interdependent self-construal, this association may be moderated by cognitive attunement to pertinent aspects of the external environment. This modulation may be expected because the reduced self-interest (as reflected in the reduced OFC volume) may be necessary, but not sufficient to yield high levels of interdependence. For example, those with reduced levels of self-interest might be apathetic and lack interest in the external environment. These individuals will be neither independent nor interdependent. We therefore hypothesize that for these individuals to achieve high levels of interdependence, they will have to exhibit an astute interest in the external environment that includes both other individuals and various social events. Only when they are perceptively vigilant of such external contingencies will they feel compelled to adjust their actions to them, thereby fostering a strong tendency toward interdependent self-construal.

Previous cross-cultural work shows that compared with European Americans, Asians are not only more interdependent (or less independent), but also more holistic in cognitive style (23). Thus, Asians attend more broadly to various objects that are in the surrounding in addition to a focal object. Indeed, some more recent studies with neuroscience methods have shown that interdependence is associated systematically with holistic attention (24). Although holistic attention could be part of the astute cognitive attunement or vigilance to external environment, it is not clear whether it fully captures the cognitive attunement to external environment, insofar as holistic attention may result from a greater propensity to be distracted by various stimuli existing in the environment. To better capture the perceptual and cognitive vigilance, or attunement, to the environment, we used a well-validated scale of the vividness of object imagery—one of three subscales of the Object-Spatial Imagery and Verbal Questionnaire (OSIVQ) (25). The OSIVQ distinguishes among three cognitive styles: object imagery, spatial imagery, and linguistic. Among these cognitive styles, the object imagery cognitive style refers to the degree to which individuals form vivid images of various objects in the environment. Sample items include, “My images are very colorful and bright,” “My images are very vivid and photographic,” and “When I imagine the face of a friend, I have a perfectly clear and bright image.” We anticipated that the link between interdependence and the reduced OFC volume would be moderated by the cognitive attunement to external environment and, thus, by the object imagery subscale of the OSIVQ. Specifically, this link would be stronger for those higher in the object imagery than those lower on this count.

To test these predictions, we performed a structural magnetic resonance imaging on 135 Japanese young adults while assessing (*i*) independent and interdependent self-construals and (*ii*) the degree to which individuals form vivid images of external objects (object imagery).

### Results

**Questionnaire Data.** Table S1 presents descriptive statistics of demographics, self-report measures, and the zero-order correlations among the measures. There were significant gender differences in interdependent self-construal [ $t(133) = -2.77, P = 0.007$ ], object imagery cognitive style [ $t(133) = -2.47, P = 0.015$ ], verbal cognitive style [ $t(133) = 3.52, P < 0.001$ ] and age [ $t(133) = -2.04, P = 0.043$ ]. Compared with women, men were less interdependent, lower in object imagery, and higher in verbal cognitive style. Also in this sample, men were somewhat younger than women.

**Voxel-Based Morphometry.** We adopted the voxel-based morphometry (VBM), a fully automated, whole-brain, unbiased, MRI-based technique capable of detecting regionally specific differences in brain tissue composition (26). VBM algorithms typically consist of the following steps: (i) segmentation of the structural images into different brain tissues to yield a map of the voxelwise probability of gray matter for each individual; (ii) macroscopic normalization of the individual gray matter images to a standard brain template so that the gray matter maps from all individuals can be superimposed; (iii) modulation, in which normalized gray matter maps are scaled by the macroscopic transformations to preserve local volumes; (iv) smoothing of the modulated images so that each voxel contains information from its neighboring voxels; and (v) voxel- or cluster-based spatial statistics across brains at every voxel (27). The VBM has been widely used (28), and its cortical volume estimates are highly correlated with cortical thickness calculated manually from every structural cortical map (29–31). We first performed a whole brain analysis using interdependent self-construal as the seed and identified brain regions whose volume is predicted by interdependent self-construal. We applied FWE corrections for multiple comparisons, which controls for the chance of any false positives (as in Bonferroni methods) across the entire volume, along with a small volume correction to reduce the number of comparisons being performed and increase the chance of identifying significant results in particular regions of interest.

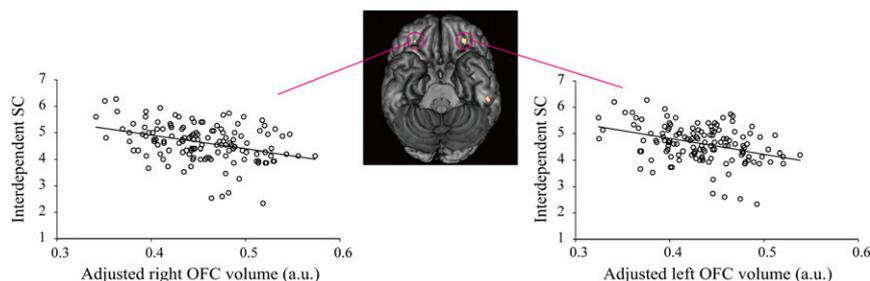
As shown in Table S2, we found negative correlations between interdependent self-construal and the gray matter (GM) volume in several brain regions. All these correlations were significant after FWE corrections. As predicted, these regions included bilateral middle OFC. A sizable region (cluster size = 31) in the left OFC was reliably linked to interdependent self-construal. Although the region of the right OFC that was linked to it was apparently small (cluster size = 4), this fact must be interpreted while considering the fact that we used a stringent set of FWE corrections. The specific OFC regions identified and the pertinent scatter plots are found in Fig. 1. Other areas that show similar associations included right fusiform gyrus, left inferior temporal gyrus, left lingual gyrus, and left postcentral gyrus. When a more lenient statistical threshold was used as in a recent study (22), a greater number of areas showed sizable correlations. However, the ones listed in Table S2 are the only ones that survived our stringent statistical threshold. These areas showed highly reliable decreases of the GM volume as a function of interdependent self-construal. On an a priori reason alone, we had no reason to expect these remaining regions to be linked strongly to interdependent self-construal. It is therefore noteworthy that the right fusiform gyrus showed the most pronounced inverse correlation with interdependent self-construal.

Notably, we found no significant correlations, either positive or negative, between independent self-construal and the GM volume in any brain regions. This null result remained unchanged even

when we used a lenient voxel-level statistical threshold ( $P < 0.001$ , uncorrected). Nor did we find any regions showing increased or decreased GM volume associated with object imagery. This null finding also remained unchanged when the lenient statistical threshold was adapted.

Next, to determine whether the present OFC findings were regionally specific, we performed a separate analysis including total brain volume (TBV) as a covariate. Here, we confined our analysis to regions of interest while using a small volume correction procedure to guard against the inflation of type I errors caused by multiple comparisons (FWE-corrected,  $P < 0.05$ ). To this end, we used anatomical masks of bilateral middle OFC created with Automated Anatomical Labeling (AAL) atlas (32) implemented in the WFU PickAtlas (Wake Forest University) (33). This analysis showed that the results for the left and right OFC remained significant [left OFC: Montreal Neurological Institute (MNI) coordinates  $-27, 42, -14$ ,  $Z$  value = 3.53; right OFC: MNI coordinates  $32, 42, -12$ ,  $Z$  value = 3.31], indicating that the present OFC findings are regionally specific, and cannot be explained by whole-brain volume differences across subjects. Following the analysis including TBV as a covariate, we also performed a separate analysis including age, sex, and TBV as covariates of interest. The association between interdependent self-construal and the left OFC GM volume remained significant (MNI coordinates  $-27, 42, -14$ ,  $Z$  value = 3.13) after small volume correction although the corresponding correlation for the right OFC GM volume was no longer significant. This finding indicates that the main findings of this study cannot simply be explained by variations in age and sex.

**Moderation by Object Imagery.** Although the VBM analysis failed to detect any significant correlation between object score and regional GM volume, our hypothesis implies that object imagery would interact with OFC volume to predict interdependent self-construal. To test this possibility, we extracted the normalized voxel values of significant clusters in the bilateral OFC and performed a moderation analysis. Data were analyzed with the SPSS macro PROCESS (34). This analysis revealed significant main effects for the left OFC volume ( $B = -5.11$ ,  $t = -4.06$ ,  $P < 0.001$ , 95% CI =  $[-7.60, -2.62]$ ) and for the object imagery score ( $B = 0.22$ ,  $t = 2.54$ ,  $P = 0.01$ , 95% CI =  $[0.05, 0.39]$ ). As predicted, it also showed a significant two-way interaction between the left OFC volume and the object imagery score ( $B = -5.71$ ,  $t = -2.81$ ,  $P = 0.006$ , 95% CI =  $[-9.73, -1.70]$ ), and regression model was significant [ $R^2 = 0.22$ ,  $F(3, 131) = 12.02$ ,  $P < 0.0001$ ]. Specifically, left OFC volume was associated with higher interdependent self-construal for those with high object imagery (1 SD above the mean,  $B = -8.74$ ,  $t = -4.99$ ,  $P < 0.0001$ , 95% CI =  $[-12.20, -5.27]$ , Fig. 2A), but not for those with low object imagery (1 SD below the mean,  $B = -1.48$ ,  $t = -0.80$ ,  $P = 0.42$ , 95% CI =  $[-5.14, 2.18]$ ). This pattern remained unchanged when we entered age, sex, and TBV as covariates ( $B = -5.86$ ,  $t = -2.81$ ,



**Fig. 1.** A scatter plot showing relationship between interdependent self-construal and OFC volume. We found significant negative correlations between interdependent self-construal (SC) and bilateral OFC volume (whole-brain FWE-corrected,  $P < 0.05$ ).

$P = 0.006$ , 95% CI =  $[-9.98, -1.74]$ ,  $R^2 = 0.22$ ,  $F(6, 128) = 5.99$ ,  $P < 0.0001$ . A similar pattern emerged when right OFC volume was used as an independent variable in regression analysis. The results revealed significant main effects of the right OFC volume ( $B = -4.47$ ,  $t = -3.84$ ,  $P < 0.001$ , 95% CI =  $[-6.78, -2.16]$ ) and the object imagery score ( $B = 0.20$ ,  $t = 2.21$ ,  $P = 0.03$ , 95% CI =  $[0.02, 0.37]$ ). The results also revealed a significant two-way interaction between the right OFC volume and the object imagery score ( $B = -3.79$ ,  $t = -2.22$ ,  $P = 0.03$ , 95% CI =  $[-7.17, -0.41]$ ), and regression model was significant ( $R^2 = 0.19$ ,  $F(3, 131) = 9.95$ ,  $P < 0.0001$ ). The right OFC volume predicted interdependent self-construal for those with high object imagery ( $B = -6.88$ ,  $t = -4.36$ ,  $P < 0.0001$ , 95% CI =  $[-10.00, -3.75]$ ; Fig. 2B), but not for those low in object imagery ( $B = -2.06$ ,  $t = -1.28$ ,  $P = 0.20$ , 95% CI =  $[-5.24, 1.11]$ ). This pattern remained unchanged when we entered age, sex, and TBV as covariates ( $B = -3.94$ ,  $t = -2.24$ ,  $P = 0.03$ , 95% CI =  $[-7.41, -0.46]$ ,  $R^2 = 0.19$ ,  $F(6, 128) = 4.98$ ,  $P < 0.0001$ ).

## Discussion

Our VBM findings provide evidence that the reduced GM volume of bilateral OFC predicts interdependent self-construal. Importantly, this association was evident only among those relatively high in object imagery as assessed by a previously validated self-report scale. The finding is consistent with our hypothesis that reduced self-interest (as indicated by the reduced GM volume of the bilateral OFC) is conducive to interdependence especially for those who are cognitively attuned to external environment and, thus, represent this environment vividly.

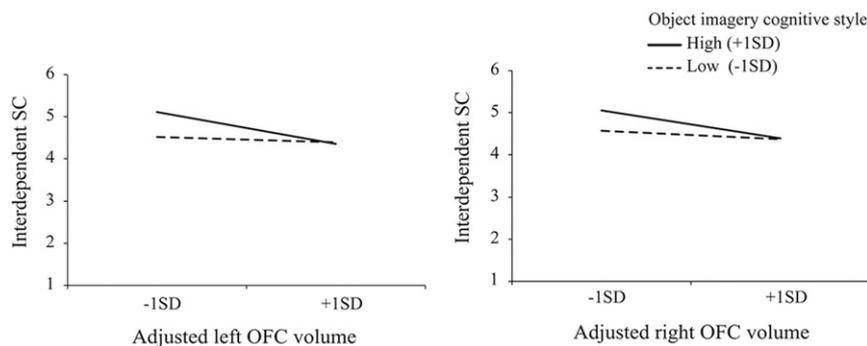
The present findings illuminate the cognitive and neural correlates of an interdependent self-construal in three key ways. First, the current evidence links interdependent self-construal to individual variation in a core cortical region responsible for value-based decisionmaking, the OFC. Future work must investigate the postulated link between the OFC GM volume and the vigor with which self-interest is pursued. Further insight could be gained by testing of focal lesion patients (12). Second, the current results indicate that the ability to construct vivid images of various objects in the environment is a “prerequisite” for the close link between reduced OFC volume and interdependent self-construal. Thus, in the absence of this ability, the reduced OFC volume may not support interdependent self-construal. Conversely, under such conditions, interdependent self-construal may not foster active down-regulation of OFC functions (e.g., personal goal pursuit and active decisionmaking). These conjectures must be tested in future work. Third, the present findings imply that people with interdependent self-construal may lower their self-interest automatically, rather than effortfully overriding their tendency to act on the self-

interest. Our results did not reveal any association between the interdependent self-construal and the GM volume in lateral prefrontal cortex—a region that is linked to successful self-control (35–37). The present results therefore take the hypothesis on interdependence a step further, indicating that lowering of self-interest is realized by automatic dispositions to reduce self-interest rather than by the active self-control (38).

Three additional aspects of our data are worthy of mention. First, the right fusiform gyrus showed the most pronounced inverse correlation with interdependent self-construal. Although unexpected, this correlation is consistent with prior work showing an inverse relationship between attentional focus and interdependent (vs. independent) self-construal (23, 24). As part of the ventral visual pathway, this region plays a significant role in developing object representations. The formation of object representations supposedly involves attention that is selectively focused on relevant objects. Second, no regions within the ventral visual pathway had any systematic relationship with the tendency to form vivid images. Although null findings are difficult to interpret, the apparent independence of object imagery from the ventral visual pathway might suggest that the salience of perceptual imagery can be enhanced through cognitive attunement or vigilance, which entails suppression of background noise so as to detect subtle cues in the environment. Third, we found no region that was correlated with independent self-construal. The particular scale of independent self-construal used in the present study might not have been fully compatible with specific ways in which this cultural dimension of independence is defined in Japan (39).

Although our analytic design involved the prediction of interdependent self-construal as a function of the cortical volume, our data are correlational and do not justify any causal inference. It is possible that the reduced OFC GM volume causally fosters interdependent self-construal (especially for those high in visual imagery). However, it is equally possible that interdependent self-construal motivates the individuals to decrease self-interest, resulting in less use of functions related to personal goals and, as a consequence, less OFC volume. The host of findings demonstrating plastic expansion of relevant cortical areas resulting from training reviewed earlier suggests that this reverse causation must be tested in future work involving interventions, longitudinal design, or both.

We should hasten to add that the linkage between brain and culture is most likely to be not only reciprocal, but also recursive and hierarchical (4, 40). One crucial consideration relates to a set of reward contingencies that are embedded in cultural practices and meanings that are organized by self-construal (41). We might assume that interdependent culture reinforces actions that promote interdependence and, thus, foster the structural change of the brain that supports such actions (i.e., interdependence → the reduction of the OFC volume). It is precisely because of this cultural influence



**Fig. 2.** Interdependent self-construal (SC) as a function of OFC volume and object imagery: Whereas interdependent SC is inversely predicted by OFC volume for those who are high in object imagery, no such relationship exists for those low in object imagery. The predicted regression values are plotted at 1 SD above and below the mean.

that the resulting structural property of the brain may render the culturally sanctioned actions more spontaneous and frequent (i.e., the reduction of the OFC volume  $\rightarrow$  interdependence). This cyclical process of mutual constitution (40) that is mediated by cultural reinforcement (41) must be systematically tested in future work.

Prior cross-cultural research shows that compared with Japanese (our current sample), Westerners tend to be more independent and less interdependent (3, 42). Extrapolating from this literature, we might anticipate that there would be a systematic cross-cultural difference in the OFC GM volume. Chee et al. (43) addressed this question by scanning both Caucasian Americans and Chinese Singaporeans, both young (age range = 18–30 y) and old (age range = 60–85 y). The researchers found a sizable cultural difference in the cortical thickness in both frontal and parietal areas (including the orbitofrontal areas) in both hemispheres for young subjects. As may be expected, the cortical thickness of all these areas was significantly greater for Caucasian Americans than for Chinese Singaporeans. The old adults showed a large reduction in cortical thickness in nearly all areas of the brain, which eliminated the cultural difference that was observed for the younger adults.

As noted earlier, Wang et al. (22) tested Chinese and found that interdependent self-construal inversely predicts the GM volume in vmPFC. The area Wang et al. identified was more medial and somewhat more dorsal compared with the OFC we found to be linked to interdependent self-construal. Keep in mind that the Wang et al. evidence apparently did not surpass the voxel-level FWE-corrected threshold. Although we found no evidence for the association between any medial PFC regions and interdependent self-construal when the FWE correction was used, we did find small clusters in the bilateral vmPFC regions (right vmPFC, MNI coordinates 11, 59, 8,  $Z$  value = 2.54, cluster size = 38; left vmPFC, MNI coordinates -5, 59, -15,  $Z$  value = 2.36, cluster size = 8) that were inversely correlated with interdependent self-construal when we substantially loosened the threshold ( $P < 0.01$  uncorrected, without any correction at either cluster or voxel level, controlling for age, sex, and TBV), consistent with the Wang et al. finding.

A possible rational behind the inverse association between vmPFC and interdependent self-construal may come from prior evidence that vmPFC is recruited in self-referential judgments that involve the formation of a cognitive representation of the personal self (44, 45). Because this cognitive representation may constitute an important part of personal goal pursuit (46), interdependence may be associated with relative down-regulation of the vmPFC function. Evidence from both Wang et al.'s and our studies seems to suggest that the predicted inverse association between the vmPFC volume and interdependent self-construal is likely to exist, but may be rather subtle and nuanced. It might be the case that the vmPFC function of developing the sense of personal self is as central for interdependent selves although interdependence often requires an active inhibition of the representations that are developed.

Potentially more problematic is the fact that Wang et al. used a rather lenient threshold and yet they failed to find any evidence that the GM volume in OFC is linked to interdependent self-construal. We speculate that reduced OFC volume is linked to increased interdependence in cultures where key components of interdependence such as obligation and duty are pitted against personal goals and preferences. Astute observers of Japanese culture over the last half century (47–49) have consistently observed that in Japan, the social as represented by “giri” (duty and obligation) and “Ninjō” (sympathy and compassion) is often juxtaposed with the personal as represented by individual preferences and goals. Importantly, there is a strong normative pressure to prioritize the former over the latter. It is possible that this form of interdependence is not always strongly upheld even within Asia. For example, it is conceivable that interdependence is achieved through personal goals that are prosocial in nature such as giving commodities to others for charity or to restore a

sense of equity. Indeed, behaviors motivated by such goals have been shown to implicate OFC and adjacent regions (50, 51). Future work should test whether the two forms of interdependence might be coexistent among Chinese (as in the Wang et al. study), whereas interdependence motivated by duty and obligation is far more prominent in Japan (as in the current work).

Lastly, a comment is warranted on the assumption that increases in the volume of certain regions reflect improved functions linked to these regions. An increasing number of training studies reviewed earlier (18, 19) has provided convincing evidence for this assumption. Nevertheless, little is known about mechanisms linking training (and the resulting expertise) to the brain volume. Moreover, no consensus exists yet about what the increased brain volume as revealed in VBM might represent both anatomically and functionally (26). Given recent advancements in social genomics (52), it stands to reason that certain epigenetic pathways are involved in regulating the cortical volume in response to specific environmental demands that are realized in the cultural reinforcement contingencies. Future work along this line may reveal the mechanisms linking culture to brain volume and then to psychological functions in much greater detail.

## Materials and Methods

**Participants.** One hundred and thirty-five right-handed Japanese volunteers (65 females and 70 males; age range 20–39 y; mean age 26.4 y) with no history of neurological or psychiatric disease were paid to participate in this study. Given the paucity of previous work testing brain volume and self-construal, we sought to at least double the typical sample size of available studies linking brain volume to various individual difference measures ( $n = 50$ –60). No participants were excluded from the analysis. The participants provided their written informed consent in accordance with the Declaration of Helsinki. The study protocol was approved by the Ethical Committee of Kyoto University.

### Questionnaires.

**Self-construal scale.** We administered the 30-item Self-Construal Scale (53), including items that measure the strength of independent (e.g., My personal identity, independent of others, is very important to me) and interdependent self-construal (e.g., It is important for me to respect decisions made by the group). Participants rated each item on a scale from 1 (strongly disagree) to 7 (strongly agree). Internal consistency of the interdependence ( $\alpha = 0.81$ ) and independence ( $\alpha = 0.82$ ) scales were adequate.

**Cognitive style.** We also administered the 45-item OSIVQ (25). The OSIVQ is a self-report questionnaire consisting of three scales for object imagery (e.g., My images are very colorful and bright), spatial visualization (e.g., I can easily imagine and mentally rotate 3D geometric figures), and verbal cognitive (e.g., My verbal skills are excellent) styles during mental imagery measured by 15 items each. Participants rated each item on a scale from 1 (strongly disagree) to 5 (strongly agree). Internal consistencies of the object imagery ( $\alpha = 0.86$ ), spatial visualization ( $\alpha = 0.74$ ), and verbal cognitive ( $\alpha = 0.52$ ) scales were adequate.

**Image Acquisition.** The participants were scanned in a 3.0-Tesla Siemens Magnetom Verio MRI scanner with a 12-channel head coil. A structural image was acquired from all participants by using a T1-weighted magnetization-prepared rapid-acquisition gradient echo pulse sequence (repetition time = 2,250 ms, echo time = 3.51 ms, inversion time = 900 ms, flip angle = 9°, matrix size = 256  $\times$  256, slice thickness = 1 mm, and field of view = 256 mm).

**Image Processing and Measurement.** The MRI data were analyzed by using VBM implemented in SPM12 (Wellcome Trust Centre for Neuroimaging), where the preprocessing steps of segmentation, bias correction, and spatial normalization are incorporated into a single generative model. The MRIs were segmented into gray matter (GM), white matter (WM), and cerebrospinal fluid (CSF) images by using SPM12 prior probability templates. The intensity nonuniformity bias correction was applied to aid segmentation by correcting for scanner-induced smooth intensity differences that varied in space. The GM images were normalized to the templates in the standard space of the MNI by using a set of nonlinear functions. A modulation step was also incorporated into the preprocessing model. Notably, spatial normalization expands and contracts some brain regions. The required modulation was performed by multiplying the warped tissue probability maps by the Jacobian determinant of the warp on a voxel-by-voxel basis, which represents the relative volume ratio before and after warping. Thus, voxel intensities in the segmented GM map, together with

the size of the voxels, reflected regional volume and preserved the total GM volume from before the warp. As a final preprocessing step, all normalized, segmented, modulated images were smoothed with a 12-mm full-width half-maximum Gaussian kernel.

Additionally, the global volumes of GM, WM, and CSF for each scan were calculated. The volume of each tissue class was estimated as the total number of voxels multiplied by the voxel size. TBV was calculated by summing the GM and WM for each subject.

**Statistical Analysis.** The preprocessed GM data were analyzed in SPM12 within the framework of the general linear model. To avoid possible edge effects around the border between GM and WM and to include only relatively homogeneous voxels, all voxels with a GM value of  $<0.05$  (of a maximum value of 1) were excluded. The threshold of significance was set at  $P < 0.05$  at the voxel level (corrected for multiple comparisons by using FWE correction), with a significance of  $P < 0.05$  at the cluster level (FWE-corrected). To avoid false-negative errors, we also used a more lenient threshold ( $P < 0.001$ , uncorrected at the voxel level, with corrections performed at the cluster level) to report the results obtained from additional analyses when necessary. Nonstationary cluster extent correction, which corrects for nonisotropic smoothness of VBM data, was also applied (54). The peak voxels of clusters that exhibited reliable effects are reported in MNI coordinates.

- Henrich J (2015) *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter* (Princeton Univ Press, Princeton, NJ).
- Tomasello M (2014) *A Natural History of Human Thinking* (Harvard Univ Press, Cambridge, MA).
- Markus HR, Kitayama S (1991) Culture and the self: Implications for cognition, emotion, and motivation. *Psychol Rev* 98:224–253.
- Kitayama S, Uskul AK (2011) Culture, mind, and the brain: Current evidence and future directions. *Annu Rev Psychol* 62:419–449.
- Smith A (2000) *The Wealth of Nations* (Modern Library, New York).
- Darwin C (1871) *The Descent of Man, and Selection in Relation to Sex* (John Murray, London).
- Kurzban R, Burton-Chellew MN, West SA (2015) The evolution of altruism in humans. *Annu Rev Psychol* 66:575–599.
- Sober E, Wilson DS (1999) *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Harvard Univ Press, Cambridge, MA).
- Fehr E, Fischbacher U (2003) The nature of human altruism. *Nature* 425:785–791.
- Rolls ET, Grabenhorst F (2008) The orbitofrontal cortex and beyond: From affect to decision-making. *Prog Neurobiol* 86:216–244.
- O'Doherty JP (2011) Contributions of the ventromedial prefrontal cortex to goal-directed action selection. *Ann N Y Acad Sci* 1239:118–129.
- Fellows LK (2011) Orbitofrontal contributions to value-based decision making: Evidence from humans with frontal lobe damage. *Ann N Y Acad Sci* 1239:51–58.
- Henrich J, et al. (2006) Costly punishment across human societies. *Science* 312:1767–1770.
- Kitayama S, Park J (2014) Error-related brain activity reveals self-centric motivation: Culture matters. *J Exp Psychol Gen* 143:62–70.
- Hughes BL, Beer JS (2012) Orbitofrontal cortex and anterior cingulate cortex are modulated by motivated social cognition. *Cereb Cortex* 22:1372–1381.
- Damasio A (2008) *Descartes' Error* (Random House, New York).
- Maguire EA, et al. (2000) Navigation-related structural change in the hippocampi of taxi drivers. *Proc Natl Acad Sci USA* 97:4398–4403.
- Draganski B, et al. (2004) Neuroplasticity: Changes in grey matter induced by training. *Nature* 427:311–312.
- Hänggi J, Brüttsch K, Siegel AM, Jäncke L (2014) The architecture of the chess player's brain. *Neuropsychologia* 62:152–162.
- Herholz SC, Zatorre RJ (2012) Musical training as a framework for brain plasticity: Behavior, function, and structure. *Neuron* 76:486–502.
- Bickart KC, Wright CI, Dautoff RJ, Dickerson BC, Barrett LF (2011) Amygdala volume and social network size in humans. *Nat Neurosci* 14:163–164.
- Wang F, Peng K, Chechlacz M, Humphreys GW, Sui J (2017) The neural basis of independence versus interdependence orientations: A voxel-based morphometric analysis of brain volume. *Psychol Sci* 28:519–529.
- Nisbett RE, Peng K, Choi I, Norenzayan A (2001) Culture and systems of thought: Holistic versus analytic cognition. *Psychol Rev* 108:291–310.
- Goto SG, Ando Y, Huang C, Yee A, Lewis RS (2010) Cultural differences in the visual processing of meaning: Detecting incongruities between background and foreground objects using the N400. *Soc Cogn Affect Neurosci* 5:242–253.
- Blazhenkova O, Kozhevnikov M (2009) The new object-spatial-verbal cognitive style model: Theory and measurement. *Appl Cogn Psychol* 23:638–663.
- Ashburner J, Friston KJ (2000) Voxel-based morphometry—the methods. *Neuroimage* 11:805–821.
- Radua J, Canales-Rodríguez EJ, Pomarol-Clotet E, Salvador R (2014) Validity of modulation and optimal settings for advanced voxel-based morphometry. *Neuroimage* 86:81–90.
- Whitwell JL (2009) Voxel-based morphometry: An automated technique for assessing structural changes in the brain. *J Neurosci* 29:9661–9664.

In the VBM analysis, the score of interdependent self-construal was entered as a covariate of interest, with the aim of identifying regions showing increased or decreased GM volume associated with interdependent self-construal. In a separate model, the score of independent self-construal was entered as a covariate of interest to identify regions showing increased or decreased GM volume associated with independent self-construal. We also explored the regions showing increased or decreased GM volume associated with the score of object imagery assessed by cognitive style questionnaire.

In addition to our primary analysis, we included TBV as a covariate to control for overall brain size across participants in a separate analysis. In addition, we also covaried age and sex, both of which are possible confounding factors for the GM volume, by entering these variables into the model in a separate analysis.

**ACKNOWLEDGMENTS.** We thank members of the Culture and Cognition laboratory of the University of Michigan for their comments on earlier versions of the manuscript and Maki Terao for her assistance in data collection. This study was conducted by using the MRI scanner and related facilities of the Kokoro Research Center, Kyoto University. This work was partly supported by the ImPACT Program of the Council for Science, Technology, and Innovation (Cabinet Office, Government of Japan), RISTEX, JST (Japan Science and Technology Agency), and National Science Foundation Grant SES 1325881. N.A. was supported by the Uehiro Foundation on Ethics and Education.

- Good CD, et al. (2002) Automatic differentiation of anatomical patterns in the human brain: Validation with studies of degenerative dementias. *Neuroimage* 17:29–46.
- Whitwell JL, et al. (2005) Magnetic resonance imaging signatures of tissue pathology in frontotemporal dementia. *Arch Neurol* 62:1402–1408.
- Davies RR, et al. (2009) Development of an MRI rating scale for multiple brain regions: Comparison with volumetrics and with voxel-based morphometry. *Neuroradiology* 51:491–503.
- Tzourio-Mazoyer N, et al. (2002) Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage* 15:273–289.
- Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003) An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage* 19:1233–1239.
- Hayes AF (2013) *Introduction to Mediation, Moderation, and Conditional Process Analysis: A Regression-Based Approach* (Guilford Press, New York).
- Tabibnia G, Satpute AB, Lieberman MD (2008) The sunny side of fairness: Preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). *Psychol Sci* 19:339–347.
- Lopez RB, Hofmann W, Wagner DD, Kelley WM, Heatherton TF (2014) Neural predictors of giving in to temptation in daily life. *Psychol Sci* 25:1337–1344.
- Heatherton TF, Wagner DD (2011) Cognitive neuroscience of self-regulation failure. *Trends Cogn Sci* 15:132–139.
- Yamagishi T, et al. (2016) Cortical thickness of the dorsolateral prefrontal cortex predicts strategic choices in economic games. *Proc Natl Acad Sci USA* 113:5582–5587.
- Vignoles VL, et al. (2016) Beyond the 'east-west' dichotomy: Global variation in cultural models of selfhood. *J Exp Psychol Gen* 145:966–1000.
- Markus HR, Kitayama S (2010) Cultures and selves: A cycle of mutual constitution. *Perspect Psychol Sci* 5:420–430.
- Kitayama S, King A, Hsu M, Liberzon I, Yoon C (2016) Dopamine-system genes and cultural acquisition: The norm sensitivity hypothesis. *Curr Opin Psychol* 8:167–174.
- Oyserman D, Coon HM, Kemmelmeier M (2002) Rethinking individualism and collectivism: Evaluation of theoretical assumptions and meta-analyses. *Psychol Bull* 128:3–72.
- Chee MWL, Zheng H, Goh JOS, Park D, Sutton BP (2011) Brain structure in young and old East Asians and Westerners: Comparisons of structural volume and cortical thickness. *J Cogn Neurosci* 23:1065–1079.
- van der Meer L, Costafreda S, Aleman A, David AS (2010) Self-reflection and the brain: A theoretical review and meta-analysis of neuroimaging studies with implications for schizophrenia. *Neurosci Biobehav Rev* 34:935–946.
- Qin P, Northoff G (2011) How is our self related to midline regions and the default-mode network? *Neuroimage* 57:1221–1233.
- Markus HR, Nurius P (2017) Possible Selves. *Am Psychol* 41:954–969.
- Benedict R (1946) *The Chrysanthemum and the Sword* (Houghton Mifflin, Boston).
- Kondo DK (2009) *Crafting Selves: Power, Gender, and Discourses of Identity in a Japanese Workplace* (Univ of Chicago Press, Chicago).
- Lebra TS (1976) *Japanese Patterns of Behaviour* (Univ of Hawaii Press, Honolulu).
- Tricomi E, Rangel A, Camerer CF, O'Doherty JP (2010) Neural evidence for inequality-averse social preferences. *Nature* 463:1089–1091.
- Moll J, et al. (2006) Human fronto-mesolimbic networks guide decisions about charitable donation. *Proc Natl Acad Sci USA* 103:15623–15628.
- Cole SW (2014) Human social genomics. *PLoS Genet* 10:e1004601.
- Singelis TM (1994) The measurement of independent and interdependent self-construals. *Pers Soc Psychol Bull* 20:580–591.
- Hayasaka S, Phan KL, Liberzon I, Worsley KJ, Nichols TE (2004) Nonstationary cluster-size inference with random field and permutation methods. *Neuroimage* 22:676–687.